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Mating strategies and monogamy in a territorial breeding anuran, *Rana dalmatina*: a result of sexual conflict?

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In anurans, sexual conflict of interest between the sexes over the mating system should be exacerbated by external fertilization and male-biased sex-ratio. However, the agile frog *Rana dalmatina* exhibits numerous monogamous characters despite a lack of parental care. Each caller was found to defend a distinct territory but, upon the female arrival, the frequency of calling males decreased. The number of observed amplexus and the number of clutches were strictly equal to the number of females. Examining sexual differences in the optimal mating system, sexual parasitism (4.2 %), synchronous polyandry (5.2 % of the clutches) and successive polygyny (4.2 %) were found as alternative strategies. Genetic polyandry was evidenced in 18 % of the clutches. Satellite activities are related to the increase of competitive interactions and result in a strong female harassment. Thus, sexual conflict influenced the development of alternative strategies. These results suggest that female multiple amplexus may be regarded as a forced mating strategy resulting in a coercive polyandry. In contrast, resulting both from the male territorial behavior and from the synchronous arrival of females, the prevalent monoandrous mating system should reduce the sexual antagonism.

INTRODUCTION

In most species, males can maximize their fitness by multiplying mates with numerous partners, whereas females cannot increase their progeny by mating with many males (BATEMAN, 1948; ARNOLD & DUVALL, 1994). This reasoning led to the hypothesis that most monogamous or monoandrous breeding systems chiefly depend upon restricted access to resources or on the need for parental care, and emphasized the role of female mate choice (WITTENBERG & TILSON, 1980; CLUTTON-BROCK, 1989; REYNOLDS, 1996). Thus, mating system and pair cooperation are affected by resource dispersion in numerous socially monogamous birds (DAVIES, 1989; KEMPENAERS, 1995). Interestingly, breeding systems have proven more perplexing than previously imagined. Thus, the reasons why animals are monogamous are unclear when no resources are defended and no parental care occurs. Furthermore, numerous recent studies have revealed a growing evidence for multiple mating in several species formerly regarded as socially monoandrous. Polyandry is found practically ubiquitous in insects (Arnqvist & Nilsson, 2000), but it was also inferred in reptiles (Madsen et al., 1992), birds (Birkhead & Møller, 1995; Hasselquist et al., 1996; Double & Cockburn, 2000) and mammals (Hoogland, 1998; Schenk & Kovacs, 1995; Wilmer et al., 2000).

Because of their external fertilization mode and their generally weak or inconsistent parental care, multiple mating and sperm competition should be common phenomena in anuran amphibians (Roberts et al., 1999). The promiscuity of males chorusing in breeding congregations (Halliday & Tejedo, 1995; Håkansson & Loman, 2004) should facilitate multiple paternities in egg masses by simple spermatic diffusion. Moreover, many anuran species exhibit a noticeable sexual size dimorphism in favor of females and a male-biased sex-ratio (Geisselmann et al., 1971; Blab, 1986; Reading et al., 1991; Lodé et al., 2005), since males arrive precociously and usually stay for a longer time than females in the breeding site. Such a male-biased sex-ratio could increase competitive interactions and may result in multiple males amplecting with a single female (Fukuyama, 1991; Jennions et al., 1992; Halliday & Tejedo, 1995). Surprisingly, only few studies referred to genetic polyandry within a single clutch in the wild although multiple amplexus were commonly reported in anurans. Polyandry as a result of multiple amplexus was revealed by DNA finger printing in *Agalychnys callidryas* (D'Orgeix & Turner, 1995). Similarly, synchronous polyandry was inferred from protein electrophoresis in *Crinia georgiana* (Roberts et al., 1999) and in *Rana dalmatina* (Lodé & Lesbarrères, 2004; Lodé et al., 2004). Moreover, multiple spawning was observed in *Leptodactylus* (Prado & Haddad, 2003) and high multiple paternity was evidenced from egg masses in *Rana temporaria* (Laurila & Seppä, 1998). It may be alleged that polyandry provides no real advantages for most anurans showing a lack of parental care (see Reynolds, 1996), but the potential for multiple genetic paternity was not often investigated.

By contrast, there are some anuran species in which multiple amplexus were rarely or never observed, so that they could be regarded as socially monoandrous species. Here monoandry refers to a female mating with a single male (but a male may have several successive amplexus), whereas monogamy corresponds to a single male mating with a single female. Thus, the agile frog *Rana dalmatina* could be thought as a typically monoandrous species, as one female releases a single clutch during the breeding season and synchronous multiple amplexus has never been reported (Geisselmann et al., 1971; Blab, 1986; Hettyey et al., 2005). It is however difficult to hypothesize how monoandry could be favoured in the absence of evolutionary advantages. Most of studies on sexual selection focused on female mate choice but the evolutionary question rests in the asymmetry of interest between the sexes, i.e., the sexual conflict (Rice, 2000). Resulting from the deviation of potential fitness of males and females, sexual conflict is virtually omnipresent and stems from competition between males for the fertilization of eggs (Rice, 2000). Genetic interest of male and female do not only diverge but, in frogs, the sexual conflict should be exacerbated by the male-biased sex ratio and the external fertilization. Agile frogs do not form choruses and, as most precocious breeding anurans, do not forage during the breeding season, so that neither resource dispersion nor the need for parental care do clearly influence their reproductive behavior and monoandry. Competition within sexes mostly leads to alternative mating strategies (TABORSKY, 1994; LUCAS & HOWARD, 1995), but the evolution of such tactics may increase the variance in reproductive success (NEFF, 2001) and therefore influence the conflict between the sexes (GAVRILETS et al., 2001; JONES et al., 2001). Consequently, it could be predicted that male and female should adopt different optimal mating strategies as a result of sexual conflict (RICE, 2000; see also LODÉ, 2006). Actually, although there is a lack of empirical studies, the sexual conflict is proved to raise an important issue in evolutionary biology (GAVRILETS et al., 2001; CHAPMAN et al., 2003), but how monogamy may reduce the sexual conflict is still hardly ever evoked.

Widely found throughout Europe, the agile frog *Rana dalmatina* is a nocturnal and terrestrial anuran which gathers in small breeding congregations during approximately 20 days from February to March. Amplexus is axillary and frog amplecting pairs are distant from each others.

By examining variations in the agile frog mating system, this paper aims at investigating whether sexual differences in optimal mating result in alternative reproductive strategies. Exploring the basis of sexual conflict, i.e., alternative strategies in male-biased frog populations, this work contributes to the understanding of the maintenance of monoandrous strategy in animals.

MATERIAL AND METHODS

MATING STRATEGIES

Field study was conducted in four breeding ponds near Redon (47°34'N, 2°50'W), western France, from 1998 to 2000. One month before the breeding period, every pond was fenced by a plastic canvas associated to buckets covered with a transparent and semi-rigid plastic. Males arrived some days earlier than females and spent more time in the pond. Captures were surveyed twice daily in order to intercept all breeding individuals. Frogs were marked (toe-clipping) and then released in the breeding pond. The breeding adult sex-ratio (ASR) was calculated as total number of males captured / total number of females captured. A quadrat with 2 m grid was set one month before in the four ponds surveyed by five observers deployed around the ponds. Frogs were located at dusk using a night optic and male locations were recorded on the quadrat map. The radius of the area of male breeding locations was estimated by measuring the distances among 72 callers. The number of caller males was estimated every night between 21 and 24 h by both auditory and visual localization by five observers, and the number of satellite males (i.e., with no calling activity) was estimated by the difference between number of callers and number of intercepted males. Samples of callers, satellites and females were hand caught, measured and immediately released. Reproductive events and aggressive behavior were monitored every night throughout the breeding season. As soon as the amplecting frogs were spawning, some animals were hand caught and measured. Every female was released after spawning. The objective of this procedure was to minimize all perturbations. The stress of frogs was considered as minimal since animals were rapidly hand caught, measured and immediately released. Every observed animal resumed normal behaviors (calling, moving or amplecting) after release.

Table 1. – Effective number of alleles (EN), observed heterozygosity (H_0) and non-biased expected heterozygosity (H_{NB}) (average ± standard deviation) in *Rana dalmatina* tadpoles collected in four ponds.

	EN	H_0	H_{NB}	*n*
Pond 1	3.33	0.4332 ± 0.061	0.5876 ± 0.056	132
Pond 2	3.33	0.3909 ± 0.120	0.5773 ± 0.072	165
Pond 3	3.33	0.4130 ± 0.125	0.5760 ± 0.065	143
Pond 4	3.33	0.4022 ± 0.099	0.5934 ± 0.083	210
Mean heterozygosity		0.4079 ± 0.094	0.5863± 0.069	650

Paternity analysis

Some eggs (less than 10 %) were randomly collected from 28 separated clutches to avoid diffuse fertilization and hatching tadpoles (*n* = 22-24 per clutch for a total of 650 tadpoles) were reared during 20 days in constant environmental conditions. Regarding ethical considerations, less than 10 % of eggs were collected to minimize the impact on frog populations as our goal was only to demonstrate multipaternity and only 22-24 tadpoles from collected clutches were instantaneously killed for genetic analysis using MS222. The others were released on the site. Paternity was inferred from allozymic data following Laurila & Seppä (1998) and Roberts et al. (1999). Polymorphic loci of offspring were analyzed by starch gel electrophoresis using standard techniques. Samples were homogenized in equal volume of distilled water and centrifuged at 10,000 g for 15 minutes at 4°C. Migration was performed using two buffer systems, Tris-citrate pH6 and Tris-EDTA-borate pH8. Slices were stained for revealing five specific enzymes encoded by six polymorphic loci with 2 to 5 alleles (tab. 1). From allozymic data, F-statistics were performed using Genetix software (Belkhir et al., Genetix@crit.univ-montp2.fr) and Popgenes 32 (Yeh et al., 1997). Allozyme phenotypes were considered evidences for heritable genotypes, and multipaternity was estimated using PAPA 1.0 (Duchesne et al., 2002). The purpose was to determine a minimal set of loci based on the expected number of parents, the possibility of sexing parents and the level of genotyping error. The parentage allocation method used in PAPA is based on the likelihood that a parental pair produces multilocus genotypes found in the tested offspring. In calculating likelihood, mating is assumed to be random and all potential parents are supposed to have equal reproductive capability. Some deviation from the latter conditions will not seriously impair the efficiency of the allocation process. Since every female produces a single clutch during the breeding season, the program PAPA simulates parental genotypes allowing estimating the minimal number of genitors for each clutch. Monoandry refers to genetic evidence of mating with a single male and polyandry with two males at least. Polygyny refers to the observation of one male fertilizing successively several clutches with no genetic evidence.

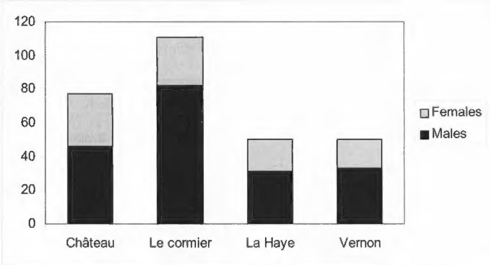

Fig. 1. – Male-biased sex-ratio in the four studied ponds as revealed by the total number of individuals intercepted.

RESULTS

MATING STRATEGIES

The adult sex-ratio was male-biased in every pond, averaging 2 males per females (SD = 0.6, ASR range 1.48-2.82, n = 288 frogs; fig. 1) with no significant differences among ponds ($\chi^2 = 4.75$, d.f. = 3, $P = 0.19$). No frogs were detected in the ponds before spring dispersal, and therefore agile frogs did not hibernate under water in ponds. As soon as they arrived, most males (78.3 %, n = 92) entered the ponds and exhibited a calling activity. Each caller defended a distinct territory ranging 2.1 m in diameter (± 0.9 m, n = 72), so that callers were widely separated, and some other males arrived progressively (total males n = 192). Male intrusions into another male calling place were followed by brief chases. Females arrived with a mean of 6.5 days later than first males, but the sex-ratio remained male-biased averaging 2.0 males for a female (SD = 0.6, range 1.48-2.82, total females n = 96). With the female arrival, the frequency of calling males decreased to reach only 52.6 % (n = 192 males; fig. 2) and breeding (amplexus) extended for 9 days until the last female departure. Numerous males (47.4 %) moved around the pond side exhibiting a satellite behavior searching for mate opportunities. The mean size of callers, averaging 47.7 mm (± 5.6 mm, n = 38), was significantly higher than the size of satellites (44.1 mm ± 4.4 mm, n = 32; $t = 2.97$, d.f. = 68, $P < 0.02$).

AMPLECTING PAIRS

The number of observed amplexus and the number of clutches were strictly equal to the number of females (n = 96). Over 83.3 % of females entered water alone and went towards the

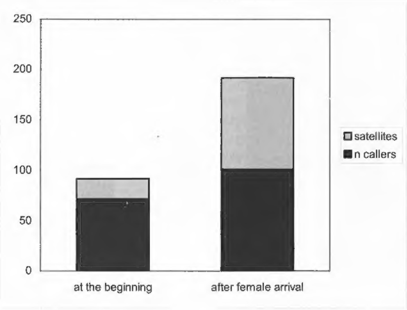

Fig. 2 – Respective number of caller and satellite males in the breeding pond at the beginning of the breeding period and after the arrival of females.

callers. However, in 16 cases (16.7 %), when a female approached the water, some male satellites tried amplecting dorso-laterally, ventrally or even over the legs of females. Hostility between sexes was evidenced since females actively rejected them. Most observed male satellites (68.8 %) gave up their amplexus attempts as soon as they intruded a caller territory or were actively rejected by the caller. After amplecting male and female left the clutch, some male satellites (4.2 %, $n = 4$ on 97) exhibited a sexual parasitism, by attempting to come above the clutch. Only five multiple amplexus on 96 (5.2 % versus 94.8% in mono-amplexus, $n = 96$) were observed for a very brief period so that the proportion of observed multiple amplexus was significantly lower than the proportions of attempts by satellites ($z = -2.544$, $P = 0.01$).

Amplecting pairs were distant from each others and females released a single clutch and then went back. The caller persisted to have a calling activity after this first amplexus during a mean of 8 days. In only four cases (4.2 %), a second female was found to consent to an amplexus with a caller which had already fertilized a clutch, realizing a successive polygyny some days after the first amplexus (mean = 3 days, range 1-5). Numerous (45 %) caller males switched for alternative behavior during the breeding period.

Paternity analysis

Five analyzed loci (*α-gdh*, *Ldh-1*, *Ldh-2*, *Mpi* and *6-Pgdh*) exhibited a pattern with at least three alleles, but enzyme *Pgm* showed a di-allelic pattern. The effective number of alleles per locus was 3.33. Among the ponds, observed heterozygosity ranged from $H_0 = 0.433$ to $H_0 =$

Table 2. – Polyandry evidences and offspring proportion resulting from a fertilization by a second male in five multiple paternal clutches as inferred from PAPA software.

	n analysed offspring	*n* estimated fathers (minimum)	Proportion of offspring corresponding to the first male	Proportion of offspring corresponding to a second male
Clutch 1	24	2	0.708	0.291
Clutch 2	24	2	0.792	0.208
Clutch 3	22	2	0.727	0.273
Clutch 4	22	2	0.818	0.182
Clutch 5	22	2	0.773	0.227
Total	114	Mean = 2	Mean = 0.763	Mean = 0.238

0.391 (tab. 2) and most loci showed significant deviation from Hardy-Weinberg equilibrium as it could be expected in samples structured into sub-samples, here clutches.

In most clutches (82.1 %, $n = 28$), paternity could be assigned to a single male per clutch using different simulations. However, for five clutches (17.9 %), a single male was unlikely to have fathered the offspring, and at least two males had shared paternity, evidencing multipaternity. In each multi-paternal clutch, a single male fertilized on average 76.2 % of the eggs whereas only 23.8 % of the eggs could be attributed to a second male, with no significant differences among clutches ($z = -1.207$, $P = 0.11$, tab. 2). No evidence for a third male fathering some tadpoles was found. Because clutches were sampled at distance from each others on different male territories, the results could not be attributable to two females. The proportion of clutches evidencing multiple paternity did not significantly differ from the proportion of satellite amplexus attempts ($z = 0.148$, $P = 0.441$) but was significantly higher than the proportion of observed multiple amplexus ($z = 2.163$, $P = 0.01$). Nonetheless, because of male pond fidelity resulted in male relatedness, multiple paternity may be higher than found. The frequency of putative successive polygyny (4.2 %) is significantly lower than the frequency of polyandry (17.9 %, $z = 2.46$, $P < 0.007$).

DISCUSSION

Sexual conflict of interest between the sexes is widely considered as an evolutionary force driving mating strategies (CARO & BATESON, 1986; GROSS, 1996; GAVRILETS, 2000; GAVRILETS et al., 2001). Indeed, interactions between sexes are recognized to influence alternative behaviors. The present study suggests that, although both synchronous polyandry and successive polygyny occurred in *Rana dalmatina*, the mating system is basically dominated by monogamous reproductive strategies, reducing sexual conflict.

Alternative strategies

In the agile frog, whereas large males (callers) defend territories based on call advertisement, other males (satellites) actively move searching for mate opportunities. Since the discovery of sexual parasitism in the tree frog (Perrill et al., 1978), callers and alternatively satellites have often been identified in breeding anurans (Howard, 1984; Arak, 1988). Male strategies can vary throughout the lifetime. Mature dominant frogs can use durable calling activities, whereas young and subordinate animals should only adopt a search for mate behavior (Loman & Madsen, 1986; Houston & McMamara, 1987; Lucas & Howard, 1995). Agile frogs do not hibernate under water in ponds before their breeding dispersal and males have to control a call area in the spawning pond. Because the cost of defending a territory depends upon the level of competition, mature males may switch for alternative behaviors if the sex-ratio is strongly male-biased. Male-biased sex-ratio was often evidenced in anuran populations (Geisselmann et al., 1971; Reading et al., 1991; Lodé et al., 2005) but was rarely documented in agile frogs (Blab, 1986). In agile frogs, callers are significantly larger than satellites but have to actively defend their exclusive breeding territory each time a satellite intrudes. Although callers show a better mating success (Lesbarrères et al., 2008), call advertisement constitutes a strong attractive cue for females but the call activity remains insufficient to exclude all satellites (Lesbarrères & Lodé, 2002). Satellites move around the pond searching for mate opportunity and try to catch any female approaching the water. Nonetheless, most satellites do not keep the benefit of this effort and have to renounce or are evicted by the caller as soon as the female arrives in a caller territory. In most cases, satellites fail amplecting but they may marginally succeed if the caller is not vindictive enough. As it was observed in other anuran species (Roberts et al., 1999), such amplexus are rarely dorsal but lateral or even ventral and therefore can only lead to a partial fertilization. Thus the satellite strategy allows certain males to partly fertilize a clutch realizing a genetic polyandry. Satellite activities should be related to the increase of competitive interactions and mainly result from mating rivalry in which males compete over access to females, some males switching to alternative behavior as soon as the first females arrive. Therefore, multiple amplexus may be regarded as a forced mating strategy resulting in a coercitive polyandry. Moreover, such simultaneous polyandrous mating do not seem to allow a better fertilization as Byrne & Roberts (1999) demonstrated in *Crinia georgiana*. Nevertheless, polyandry may be also thought of as a result of a secondary fertilization. Some satellite males show a sexual parasitism trying to fertilize the clutch of another pair. Jennions & Passemore (1993) demonstrated the capability of sperm release by a second male in *Chiromantis*. Although in *Rana dalmatina* male territorial behavior perseveres and leads to a guarding behavior, such a secondary fertilization may explain the apparent discrepancy between the apparent number of multiple amplexus and the frequency of multiple paternity. Actually, multiple paternity should be underestimated in agile frogs both because allozymic variations are not the best genetic marker for polyandry and because of the breeding site fidelity of most anurans (see Reading et al., 1991). Breeding site fidelity should result in increasing relatedness of breeding adults.

Anyway, whether multiple mating results from forced mating or secondary fertilization, the polyandry should restrict the evolutionary influence of female mate choice and reduce the opportunity for sexual selection (see Jones et al., 2001). However, the females actively move towards a caller territory. Although females go to breeding territories where no female laid a clutch, alternatively some females may have amplexus with a polygynous male. Such polygyny consists in a successive polygyny since these females release their clutch in the same territory where a male fertilized a first clutch a few days ago The reason why those females appeared to avoid mating with a previously mated male is not clear. In numerous fish species, females are more attracted by a male which guarded a clutch (BISAZZA & MARRCONATO, 1988; WARNER et al., 1991). But, in the agile frog, polygyny occurs marginally and may be interpreted as a prudent strategy performed by an inexperienced female by copying the behavior of an experienced female (SIROT, 2001). Anyway, the relative synchrony of spawning events restricts their opportunity to mate with a previously mated male Moreover, the rareness of this strategy suggests that it is little efficient for improving the fitness. Females may restrain their polygyny to avoid the competition risk unfavorable to the tadpoles of the second clutch. Negative competitive interactions in tadpoles were widely reported (WILBUR, 1982, TRAVIS, 1984, GRIFFITHS, 1991; FARAGHER & JAEGER, 1998, BARNETT & RICHARDSON, 2002). Moreover, hatched after the first, these tadpoles may suffer cannibalism from tadpoles of the first clutch (CRUMP, 1983).

THE RESULTING MATING SYSTEM

Although multiple paternity was found in at least four distinct anuran species (D'ORGEIX & TURNER, 1995, LAURILA & SEPPÄ, 1998; ROBERTS et al., 1999; LODÉ & LESBARRÈRES, 2004), their mating behavior greatly differed The territorial defense of an exclusive individual breeding site promoted the prevalent monoandrous character of the agile frog Indeed, both polyandry and polygyny were found to be marginal strategies and agile frogs exhibited numerous monogamous characters. As illustrated by numerous bird species (DAVIES, 1989, SANDELL, 1998), it has been proposed that female competition was the key factor for the evolution of monogamy (the female aggression hypothesis, WITTENBERG & TILSON, 1980). Nonetheless, antagonistic interactions hardly ever occurred in monogamous females and seemed unlikely to produce the frog monogamy Mainly based on mammals, it has been also argued that monogamy evolves due to the need for parental care (CLUTTON-BROCK, 1989) Association between males and females may provide both a best feeding and safety to the progeny. Nevertheless, that monogamy was promoted by parental care was rarely supported by investigations on mating systems and was only found as special cases (KOMERS & BROTHERTON, 1997). The level of sociality of mammal females is the main parameter which influenced the male capability to control them (EMLEN & ORING, 1977, BROTHERTON et al., 1997), and KOMERS & BROTHERTON (1997) proposed that monogamy in mammals is basically due to their solitary habits rather than the need for parental care Relating monoandry to female arrivals and dispersion of breeding males, our results suggest that monoandry in anuran is chiefly associated with the territorial breeding behavior of males and with the relative synchrony of females arrivals. Using small exclusive breeding territory, the male behavior followed the prediction that sexual territory should be small enough to allow males to defend them

Actually, any deviation from monogamy results in an increase of sexual conflict, since in a monogamous mating system any trait that enhances the fitness of one sex also improves the fitness of the other. The main advantage of monogamy is that both male and female produce most offspring whereas polygyny results in better success only in some males. Whereas sexual differences in mating may result in alternative reproductive strategies, the optimal response of agile frogs to the sexual conflict converges towards a monogamous breeding system achieving a sexual equilibrium. Resulting both from the male territorial behavior and from the synchronous arrival of females, the prevalent monogamous mating system reduces the sexual conflict. The reason why frogs adopt a monogamous mating system may be related to the fact that monogamy yields genetic benefits.

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